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CONTRIBUTIONS ON THE MORPHOLOGY OF THE ACTINOZOA.

IV. ON SOME IRREGULARITIES IN THE NUMBER OF THE DIRECTIVE MESENTERIES IN THE HEXACTINIÆ.[1]

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THE discovery of three of the principal features of the morphology of the Hexactiniæ, — the hexamerous arrangement of the mesenteries, their association in pairs, and the occurrence of directives, — we owe to several observers. Ehrenberg ('34) was, I believe, the first to note the hexamerous arrangement; the association of the mesenteries in pairs was first discovered by Erdl ('42) but fully worked out by Hollard ('51) a few years later; while the occurrence of directives was first observed by Thorell ('58), and more fully described by Schneider and Rötteken in 1871. The study of numerous species has demonstrated the general occurrence of these three characteristics, which may be regarded as normal for the group, but departures from the normal arrangement have also been observed. Thus, instead of hexamerism, a decamerous or an octamerous symmetry may obtain; indeed, one of the earliest thorough studies of members of the group, namely that by Hollard, was made upon a decamerous form. So too, although two pairs of directive

[1] Nos. I–III of these Contributions were published in the *Journal of Morphology*, vols. iv and v.

mesenteries are usually present, nevertheless, in a number of cases, a reduction to a single pair has been observed, not only in the Halcampidæ, but also in other less primitive families, and more especially in the Sagartidæ.

This condition, which is associated with a corresponding reduction of the number of siphonoglyphes, was observed by Thorell ('58) and has been studied more recently by A. F. Dixon ('88), Carlgren ('93), and Parker ('97). I have made some observations on monoglyphic specimens of Metridium marginatum, but Parker's observations on the same species have been so much more extensive that a record of my results seems unnecessary, as they throw no additional light on the significance of the abnormality.

The reverse condition, an increase in the number of the directives beyond the normal, is apparently much less frequent, and has, up to the present, been described only by G. Y. and A. F. Dixon ('89) in Bunodes thallia, and by Parker ('97) in Metridium marginatum. Parker found three siphonoglyphes and three pairs of directives in only *one* out of one hundred and thirty-one specimens ; but in four specimens of Bunodes thallia the Dixons found that one had two pairs of directives, one *three* pairs, one *four* pairs, and one only one pair. In the Bunodes as in the Metridium the siphonoglyphes corresponded in number with the directives, and furthermore it is to be noted that an irregular arrangement of the mesenteries was also found in all the specimens which presented what may be termed, following Parker's nomenclature, a polyglyphic condition. An increase in the number of siphonoglyphes has also been found in two other species and probably denotes a corresponding increase of directives ; the Dixons ('91) describe the occurrence of three grooves in a specimen of Metridium dianthus, and Haddon and Shackleton ('93) state that from two to seven (!) siphonoglyphes occur in different specimens of Condylactis Ramsayi.

I have recently had the opportunity of examining a species in which the number of the directives seems to be as a rule increased above the normal. This is the form originally described by Verrill ('83) as Sagartia spongicola, several speci-

mens of which I found in a collection from the West Indian seas made by the Bahama Expedition of the State University of Iowa. I have been able to compare the specimens with some kindly sent me by the U. S. Fish Commission; and in all have examined seven specimens, each of which showed abnormal arrangements of the mesenteries. Three cycles of mesenteries occur, the members of the first cycle alone being perfect; and the third cycle is sometimes incomplete. I give below in tabular form a statement of the arrangement of the perfect pairs of mesenteries in each specimen, those pairs which are directives being indicated by the letter D.

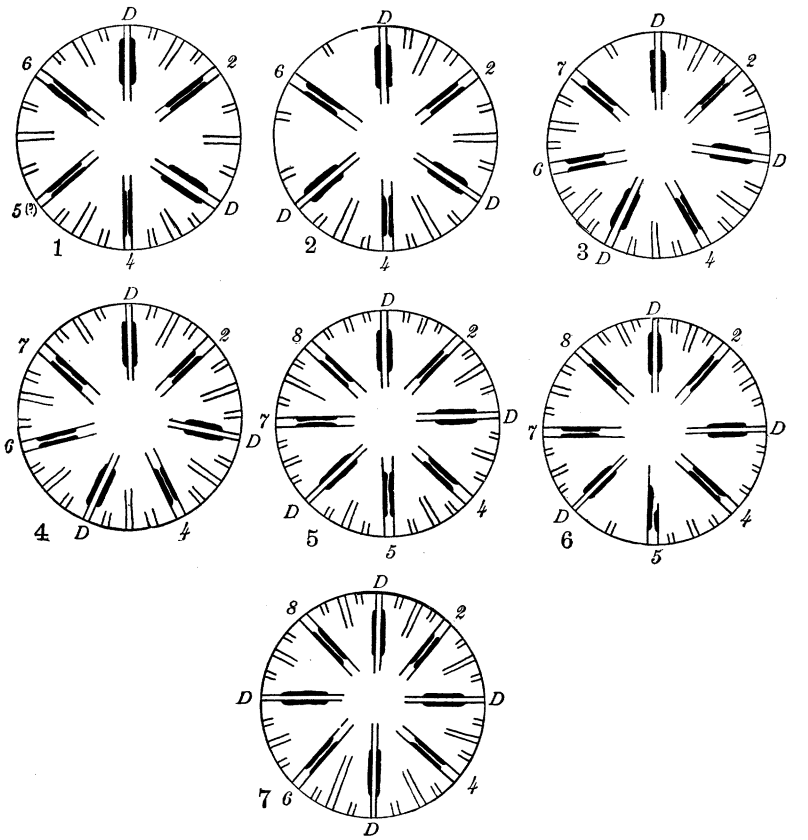
Specimen No. 1	D—2—D—4—5—6
" No. 2	D—2—D—4—D—6
" No. 3	D—2—D—4—D—6—7
" No. 4	D—2—D—4—D—6—7
" No. 5	D—2—D—4—5—D—7—8
" No. 6	D—2—D—4—5 (?)—D—7—8
" No. 7	D—2—D—4—D—6—D—8

In drawing up this table I have in all cases started with a directive, though it is of course impossible to say that in each case the tabulation has commenced with the same mesentery. Specimen No. 6 was received from the U. S. Fish Commission, the rest are from the Iowa University collection.

It will be seen from this table that of the seven specimens two are arranged on the hexamerous plan, two on a heptamerous plan, and three on an octamerous, though with regard to specimen No. 6 it is not quite certain whether the pair numbered 5 belongs to the first or second cycle, its relations to adjacent second and third cycle mesenteries indicating, however, its probable membership in the first. Furthermore it will be noticed that in one specimen there are two pairs of directives, which, however, are not opposite each other but are separated by only a single pair of the first cycle ; in five specimens there are *three* pairs of directives, and in one specimen *four.* It is possible that specimen No. 1 should be credited with three pairs of directives, since there is some uncertainty concerning the pair of mesenteries numbered 5, one member

of which appears to have its longitudinal muscles on its endocœlic surface, while in the other they appear to be on the exocœlic side.

In order to show the arrangement of the directives more perfectly, as well as the relations of the mesenteries of the second and third cycles, I give below a diagrammatic representation of a transverse section of each of the specimens examined.



A complete absence of all directives has been described by Boveri ('**93**) for the genus Gyractis; and for the reception of this form he has proposed an order Holactiniæ, considering the radial arrangement of the mesenteries which the absence of the directives brings about, sufficient to warrant the separation of forms showing it from the "biradial" Hexactiniæ.

Boveri traces these forms back phylogenetically to a stage antecedent to the appearance of the mesenteries in cycles and in pairs, *i.e.*, to a stage where the mesenteries developed, as in the Edwardsiæ, simply and bilaterally. By the development of two mesenteries on each side, the Edwardsia stage was brought into an hexactinian condition, and the formation of another mesentery on each side of one of the Edwardsian directives produced the Scytophorus condition. A further continuation of this process, the development of another mesentery on each side of the other pair of directives, resulted in the Holactiniæ, which, it must be assumed, later acquired a tendency to develop additional mesenteries cyclically and in pairs as do the Hexactiniæ.

Boveri consequently assumes the actual persistence of the Edwardsian directives in both Scytophorus and Gyractis, the absence of one pair in the former genus and of both pairs in the latter being only apparent. With his views as to Scytophorus I fully coincide, but believe that in Gyractis we have to deal with an hexactinian in which both pairs of directives have disappeared, — just as one pair has disappeared in numerous specimens of Metridium marginatum, the mesenteries which really represent them having developed their longitudinal muscles on adjacent faces.

On reading Boveri's paper I recalled the fact that I had been unable to make out directive mesenteries in Ricordea florida ('**89**), and I again subjected my preparations of that form to a close scrutiny. The stomatodæum of this species is oval, its walls having numerous longitudinal ridges, but there are no siphonoglyphes. Owing to the disc-like form of the column and the moulding of the base over the irregularities of the surface to which the animals attach themselves, it proved difficult to obtain perfectly satisfactory transverse sections of the entire column. In two cases, however, I succeeded in getting sections from which I could be reasonably certain as to the presence or absence of directives ; in one case I found *no* directives and in the other a single pair, which, however, was not opposite the end of the long axis of the stomatodæum, but to one side of it.

With these results I turned to the related genus Rhodactis and examined three specimens of R. Sancti-Thomæ. In my original description ('89) of this form I described one pair of directives as being present, and somewhat hastily assumed the presence of the second pair, though I could not be sure of its existence. A further examination showed that in one specimen but a single pair of directives was present and that pair was situated some distance from the end of the long axis of the stomatodæum ; in a second specimen one pair was again present, also to one side of the axis of the stomatodæum, but at the opposite end of the stomatodæum there was some irregularity in the arrangement of the mesenteries, and I could not be certain that a second pair of directives was not present there ; and finally in a third specimen I found *no* directives, though here again, owing to certain mesenteries not being cut exactly transversely, it is impossible to affirm their absolute non-existence.

These results, especially those obtained from Ricordea, seemed to me to have considerable bearing on the validity of the proposed order Holactiniæ. Recently two other observations of forms lacking directives have been recorded. Haddon and Duerden ('96) failed to find directive mesenteries in Cystiactis tuberculosa, and Kwietniewski ('97), finding none in Thalassianthus senckenbergianus and T. aster, has established for these forms an order Thalassianthæ. We have, then, four different genera belonging to as many distinct families, according to the usual classification, and yet presenting the essential peculiarity upon which the new order is based. If the order is a valid one, then we must separate Gyractis from the Bunodidæ, which it seems to resemble most nearly. Ricordea must be removed from its association with Rhodactis, to which it is closely related even in its histological peculiarities ; Cystiactis must be regarded as belonging to an entirely different group from Alicia ; and Thalassianthus must be placed in a new order even though it should prove necessary to separate it from Actineria. But this is not all. We must place one specimen of Ricordea florida in the new order and leave another among the Hexactiniæ, and we must similarly place one specimen of

Thaumactis medusoides (Fowler, '88) in the new order and leave the other out; and so with Sagartia undata (Carlgren, '93). This, it seems to me, is a *reductio ad absurdum.*

The complete absence of directives is not necessarily a phylogenetic peculiarity, but one extreme of the same tendency to an irregularity in the number of the directives of which many examples are now known. There seems to be no more reason for considering the complete absence of directives a peculiarity of ordinal importance than there is for so regarding their reduction to a single pair or their increase to three or four pairs. It is rather a peculiarity which is essentially individual, possibly rising secondarily in some cases to the value of a specific or even a generic character, and to regard it as of ordinal value is, it seems to me, inconsistent with our present ideas as to the phylogeny of the Anthozoa.

In conclusion it may be pointed out that the irregularities which have been described in the arrangement of the mesenteries of Gyractis and Thalassianthus are just what might be expected to occur in connection with the absence of directives, since we usually find considerable departure from the normal arrangement even in forms which lack only one pair (*cf.* Thorell, '58, Carlgren, '93, and Parker, '97).

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